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A NEW LATE MIOCENE BALAENOPTERID WHALE (CETACEA: MYSTICETI), *PARABALAENOPTERA BAULINENSIS*, (NEW GENUS AND SPECIES) FROM THE SANTA CRUZ MUDSTONE, POINT REYES PENINSULA, CALIFORNIA

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A fossil balaenopterid whale, *Parabalaenoptera baulinensis*, new genus and species, is named on the basis of a partial skeleton that was collected from the Late Miocene Santa Cruz Mudstone at Bolinas Point, Point Reyes Peninsula, California. Diatoms from the Santa Cruz Mudstone indicate an age of 6.8 to 6.0 Ma. The skeleton includes the cranium, dentaries, cervical and dorsal vertebrae, pectoral limb bones, and ribs, and the animal is estimated to have been 10 m in length when alive. The skull of *Parabalaenoptera baulinensis* has pronounced interdigitation of the rostral and cranial elements and an abrupt slope from the intertemporal region to the supraorbital process, indicating that it is a balaenopterid. However, the elongate and very narrow nasals, narrow intertemporal region, long and posteriorly tapering ascending processes of the maxillae, conspicuously elevated or swollen anterior portions of the parietals, short postglenoid processes, and long and sloping coronoid crest of the dentary distinguish *P. baulinensis* from fossil and Recent members of the subfamilies Megapterinae and Balaenopterinae. Its unique characters indicate its separation at the subfamily level, and we assign it to the new subfamily Parabalaenopterinae.

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Marine vertebrate remains occur within the Santa Cruz Mudstone exposed at the southern tip of the Point Reyes Peninsula, California (Fig. 1), where rapid erosional retreat of the coastal cliffs frequently uncovers fossils. Galloway (1977) reported fragments of whale bone and an unidentified skull, possibly that of a cetacean or sirenian, and Domning (1978) reported a dugongid sea cow from these exposures. From farther north on the Point Reyes Peninsula, in the same formation, Barnes (1976) reported a sperm whale (cf. *Scaldicetus* du Bus, 1867); a small rorqual (cf. *Burtinopsis* Van Beneden, 1872); Wilson (1937) reported a dolphin; and Repenning and Tedford (1977) reported an imagotariine pinniped (pseudo-sea lion).

The Bolinas Point area has yielded two major discoveries, relatively near each other, only about 375 m apart. The dugongid sea cow reported by Domning (1978) was found in 1972. The second specimen, discovered 12 August 1976 by the senior author, began with the serendipitous discovery of a vertebra that had eroded from the cliff about 10 m above the beach. Further excavation along the cliff face yielded the partial skeleton of the balaenopterid which is the subject of this paper. We describe this fossil balaenopterid herein and name it as a new genus and species in a new subfamily of the family Balaenopteridae.

MATERIALS AND METHODS

The location of the holotype skeleton in the sea cliff made its excavation difficult. Collection was dangerous because of the steepness of the cliff face (10 m above the beach), frequent landslides due to the crumbly nature of the mudstone, and strong surf action against the cliff face during high tides. To solve the problem of recovery, we decided to remove the fossil bone as pieces were sequentially (and naturally) exposed in the rapidly retreating cliff face. During preliminary excavation we found that the vertebral column and skull were in no immediate danger of erosion. The entire collecting process required weekly, and sometimes daily, monitoring of the site over a period of ten years.

Excavated fossil pieces, sometimes encased within the mudstone matrix, were brought to the College of Marin Biology Laboratory in Kentfield, California, for preparation. Removal of the bone from the surrounding matrix was time-consuming due to the highly fractured condition of the fossil, its variable state of preservation, and the hardness (cementation) of the rock. Small fossil fragments were bonded with white glue or Glyptal cement. An epoxy compound proved to be most effective for the larger pieces, especially the dentaries. Final reconstruction of the entire specimen was completed in 1986.

The skull and dentaries were not assembled as single units, but as closely fitting blocks or sections that can be easily disassembled for study. The assembled skull rests on a fiberglass cradle with the dentaries alongside (Fig. 2).

The descriptive anatomical terminology and measurements (e.g., Tables 1–8) follow Kellogg (1922, 1928, 1931, 1934) and Miller (1923). The classification follows that of Barnes, Domning and Ray (1985) and Fordyce and Barnes (1994). The anatomical drawings were made by a grid and measurement method. The authors and dates of publications are provided for all cetacean taxa, and those of all fossil taxa are listed in the LITERATURE CITED. The estimate of body length (10 m) was made by taking the mean of Howell's (1930:146) formula for rorquals, based on the length of the cervical series of vertebrae.

The abbreviation CASG is for the Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U. S. A.

Abbreviations used in the figures are as follows:

apm - ascending process of maxilla
bc - basioccipital crest
cc - coronoid crest
Bo - basioccipital bone
cp - coronoid process of dentary
eam - channel for external auditory meatus
Eoc - exoccipital bone
fm - foramen magnum
fn - nutrient foramina
Fr - frontal bone
ft - temporal fossa
gf - glenoid fossa
Mx - maxillary bone
n - naris
Na - nasal bone
Oc - occipital bone
occ- occipital condyle
Pa - parietal bone
Pal - palatine bone
pgp - postglenoid process
Pmx - premaxillary bone
pp - posterior process of periotic
sop - supraorbital process of frontal
Sq - squamosal bone
Tb- tympanic bulla
Vo - vomer bone
zyg - zygomatic process of squamosal

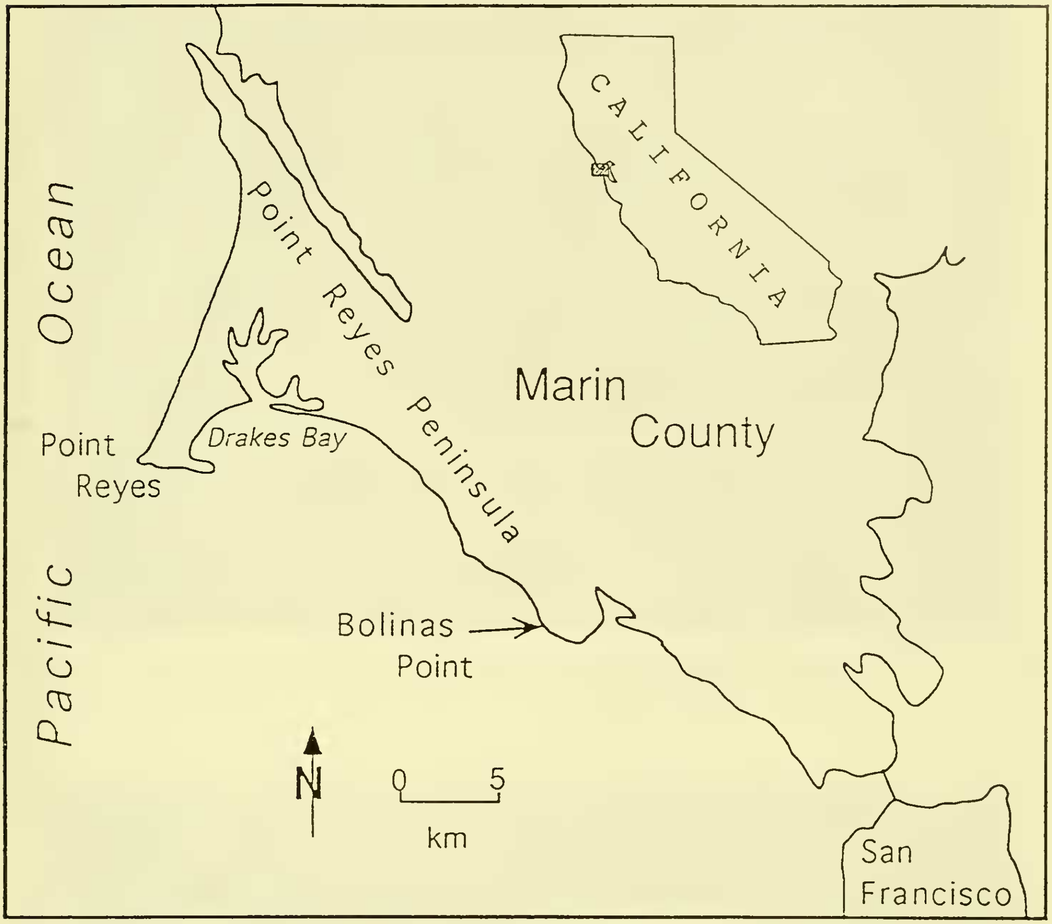

FIGURE 1. Type locality of *Parabalaenoptera baulinensis*, new genus and species, indicated by arrow, at Bolinas Point, Point Reyes Peninsula, Marin County, California.

SYSTEMATICS

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Suborder Mysticeti Flower, 1864
Family Balaenopteridae Gray, 1864

INCLUDED SUBFAMILIES. — Parabalaenopterinae, new subfamily; Megapterinae (Gray, 1866) Gray, 1868; and Balaenopterinae (Gray, 1864) Brandt, 1872.

Parabalaenopterinae, new subfamily

DIAGNOSIS OF SUBFAMILY. — A subfamily of the family Balaenopteridae differing from Megapterinae and Balaenopterinae by having cranium with a transversely narrower intertemporal region; nasal bones elongate (approaching a length to width ratio of 4:1), narrow, and nearly parallel-sided, terminating anterior to the level of the antorbital notch, rather than short, terminating posterior to the antorbital notch, and distally wide; ascending process of maxilla tapered posteriorly rather than lobate or expanded transversely; exposure of frontals on dorsal surface of intertemporal region between apex of occipital shield and posterior ends of nasals, premaxillae, and maxillae nearly twice as wide anteroposteriorly; parietals on either side of cranial vertex swollen and elevated above level of adjacent frontals; postglenoid process of squamosal short,

TABLE 1. Measurements (in mm) of cranium of holotype of *P. baulinensis*, new genus and species.

1. Greatest length of skull, anterior end of right premaxilla to level of posteroexternal angles of exoccipitals	2240±
2. Distance between anterior end of right premaxilla and apex of supraoccipital shield	1700±
3. Distance between posterior angles of exoccipitals to apex of supraoccipital shield	540
4. Distance from apex of supraoccipital shield to posterior end of left nasal bone	50
5. Transverse distance between outside margins of premaxillae at level of anterior ends of nasal bones	94
6. Maximum width of right premaxilla at level of anterior end of right maxilla	80
7. Transverse diameter or rostrum at level of widest point of nasal fossa	620±
8. Greatest anteroposterior diameter of left supraorbital process	440
9. External anteroposterior diameter of left supraorbital process	210
10. Transverse diameter of cranium between outer surfaces of zygomatic processes	980
11. Transverse diameter of cranium between margins of exoccipitals	690
12. Width of occipital condyles	198
13. Distance from upper margin of formen magnum to apex of supraoccipital shield	455
14. Vertical distance from basioccipital to level of apex of suproccipital shield	250±
15. Distance from anterior margin right zygomatic process to posterior margin exoccipital	360
16. Distance from anterior margin left zygomatic process to posterior margin exoccipital	475
17. Greatest breadth of basioccipital between inner surfaces of notches for jugular leash	248
18. Greatest length of right palatine bone	490±
19. Greatest width of combined palatine bones, anteriorly	275±
20. Greatest height of left occipital condyle	131
21. Greatest width of left occipital condyle	76
22. Vertical diameter of foramen magnum	93
23. Transverse diameter of foramen magnum	64
24. Greatest width of basioccipital between tympano-periotic processes	245

extending only slightly ventral to the ventral surface of the basioccipital crest; and dentary with long, sloping coronoid crest approaching coronoid process rather than an abruptly ascending coronoid process; coronoid process with a spindle-shaped, posteriorly-directed apex; and anterior margin of mandibular foramen smooth, lacking notch.

Parabalaenoptera, new genus

DIAGNOSIS OF GENUS. — Because the subfamily Parabalaenopterinae is at present monotypic, the diagnosis of the genus shall remain identical to that of the subfamily Parabalaenopterinae until further genera are diagnosed in the subfamily.

TYPE AND ONLY INCLUDED SPECIES. — *Parabalaenoptera baulinensis*, new species, Late Miocene of California.

ETYMOLOGY. — From the Greek *para*, for beside; plus *balaenoptera*, from Latin *balaena*, for whale, and Greek *pteron*, for fin; in reference to the apparent separation between this taxon and the lineage that includes the living balaenopterine whales.

Parabalaenoptera baulinensis, new species
(Figs. 2–7, 8b)

DIAGNOSIS OF SPECIES. — Because the genus *Parabalaenoptera* is at present monotypic, the diagnosis of the type species, *Parabalaenoptera baulinensis*, shall remain identical to that of the genus *Parabalaenoptera* until further species are diagnosed in the genus.

HOLOTYPE. — CASG 66660, a partial associated skeleton consisting of most of the cranium with tympanic bullae and periotics, both dentaries, fragments of the left scapula, both humeri, 23 vertebrae in varying states of preservation, including 7 cervicals, 15 thoracic vertebrae, a lumbar vertebra, and numerous sections of incomplete ribs.

FIGURE 2. *Parabalaenoptera baulinensis*, new genus and species, assembled holotype cranium and dentaries, CASG 66660, oblique anterodorsolateral view.

FIGURE 3. *Parabalaenoptera baulinensis*, new genus and species, oblique anterodorsal view of part of holotype skull, CASG 66660, showing elongate nasal bones.

TYPE LOCALITY. — The sea cliff, above the high tide mark near Bolinas Point (37° 54′ 6″ N, 122° 43′ 15″ W), Point Reyes Peninsula, Marin County, California, U. S. A (Fig. 1).

FORMATION AND AGE. — Santa Cruz Mudstone, of latest Miocene age, between approximately 6.8 and 6.0 Ma.

The holotype skeleton of *Parabalaenoptera baulinensis* was parallel to the bedding planes in shale of the Santa Cruz Mudstone, dipping 45° to the southwest. The interbedded siltstone contains faint parallel laminations in beds ranging from 5 to 25 cm thick. Concretions and carbonate-cemented horizons are common and occur parallel to the bedding planes. Formerly considered part of the Monterey Formation, these rocks are now assigned to the Santa Cruz Mudstone (Clark et al. 1984).

Although not abundant, fossils such as gastropods, pelecypods, echinoderms, isopod fragments, crab claws, decapod shrimp parts, fish teeth and bones, and isolated mammal bones have been collected from this formation. Many of the fossils, including the fossil whale, are better preserved in the carbonate-cemented concretions, although fossils occur throughout the Santa Cruz Mudstone. Fossil mollusks in the same strata as the holotype of *Parabalaenoptera baulinensis* were tentatively identified as limids, possibly *Acesta* sp. These bivalves generally require water depths of 500 m and water temperatures of 8°C or less (Ellen J. Moore, Branch of Paleontology and Stratigraphy, U. S. Geological Survey, Menlo Park, California, 5 May 1984, pers. comm.).

An assemblage of fossil diatoms was recovered from carbonate concretions in the same bedding plane adjacent to the fossil whale. The diatom assemblage is assignable to "Subzone A" of the Late Miocene *Nitzschia reinholdi* Zone, and implies an estimated age of 6.8 to 6.0 Ma for the fossil whale (John A. Barron, Branch of Paleontology and Stratigraphy, U. S. Geological Survey, Menlo Park, California, 10 January 1985, pers. comm.).

ETYMOLOGY. — The species name, *baulinensis*, is in reference to the type locality at Bolinas Point, Point Reyes Peninsula, Marin County, California; Bolinas is named after and was part of the 1860 historical land title of Rancho las Baulines.

DESCRIPTION. — **Cranium.** — Characters that distinguish the cranium of *Parabalaenoptera baulinensis* from those of *Balaenoptera* Lacépède, 1804, and *Megaptera* Gray, 1846, are: the more narrow intertemporal region (Figs. 4, 6), the long and narrow nasals (Figs. 3, 4, 6), and the laterally swollen and elevated portions of the parietals on either side of the intertemporal region (Fig. 7b).

The entire rostrum is not preserved and some large sections are missing. In order to estimate the original total length of the skull, we calculated the ratios of rostral length to total skull length in large extant species of rorquals. The average of these gives a rostral length that is approximately 74% of the total skull length. We applied this ratio to the fossil to obtain its estimated original skull length and body length.

The rostrum is very flat and gradually increases in depth posteriorly. The lateral margin of the maxilla is thin and blade-like. The maxilla thickens medially as it curves medially and ventrally to enclose the vomer.

The distal ends of the premaxillae are missing anterior to the distal ends of the maxillae (Fig. 6). The portion of the left premaxilla anterior to the narial opening has been pressed ventral to and against the right premaxilla as a result of geologically induced right-lateral compression of the cranium. In life, these bones were definitely separated, and probably somewhat parallel, up to their point of divergence at the anterior margin of the vertical orientation as they delineate the long, broad narial fossa. Lateral to the nasals, the premaxillae become progressively narrower posteriorly, only being 10 mm wide at the posterior ends of the nasals, and terminate 45 mm from the apex of the supraoccipital.

The maxillae are fractured and are missing some portions on their lateral margins (Fig. 6). What is preserved of the rostrum indicates that it was very broad, not arched anteroposteriorly, and that its lateral margins were thin and curved ventrally. The posterior parts of the rostral margins are fragmentary and their exact relationship to the antorbital processes is difficult to determine. The long, ascending (posterior) processes of the maxillae, overlapping and penetrating the frontals, are cuneate in shape, tapering gradually posteriorly to within 30 mm of the anterior margin of the supraoccipital, and are each 15 mm

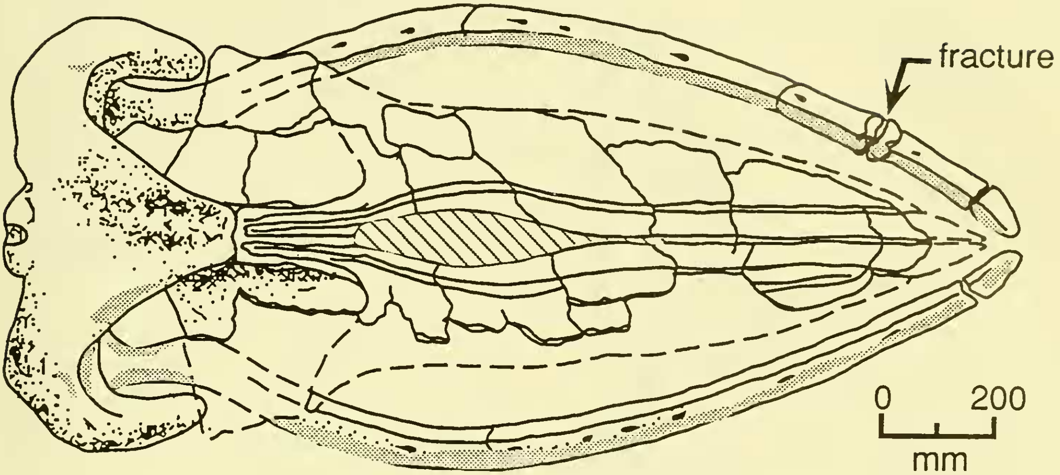

FIGURE 4. *Parabalaenoptera baulinensis*, new genus and species, dorsal view of holotype cranium and dentaries, CASG 66660; fractured area of left dentary, discussed in text, is indicated.

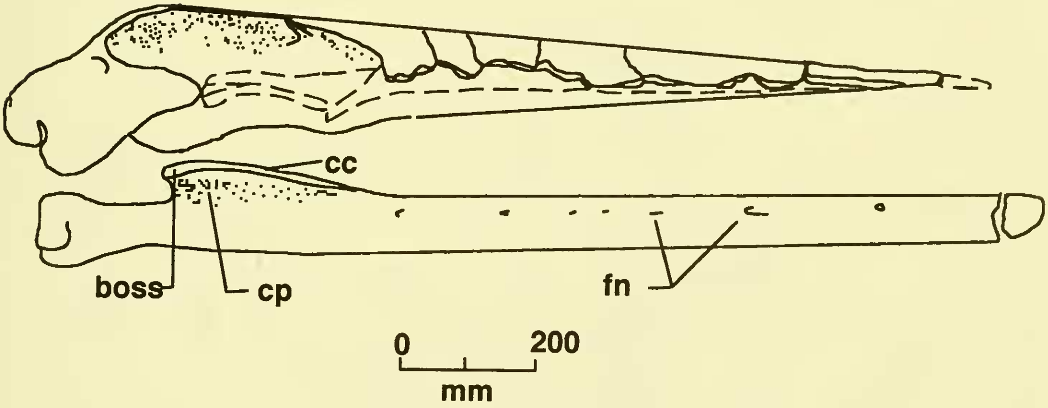

FIGURE 5. *Parabalaenoptera baulinensis*, new genus and species, lateral view of holotype cranium and right dentary, CASG 66660; see MATERIALS AND METHODS for abbreviations.

wide at the level of the posterior margin of the nasals.

The nasals (see Figs. 3, 6) are distinctive by being extremely long (maximum length = 250 mm) and narrow for a balaenopterid, and this is a primitive character. Their combined anterior width, as preserved now is 57 mm, but we estimate that this width was 64 mm prior to geologic distortion. The combined posterior transverse width of the nasals is 29 mm. The nasal bones are tightly wedged between the ascending processes of the premaxillae, and terminate 50 mm from the apex of the supraoccipital.

The length-to-anterior width ratio of the combined nasals is approximately 4:1 (Fig. 3). By contrast, among the living balaenopterids, this ratio ranges from approximately 2:1 in *Balaenoptera borealis* Lesson, 1828, (Sei whale; see Fig. 8c), to approximately 1:1 in *Balaenoptera physalus* (Linnaeus, 1758) (fin whale; see Fig. 8d), which has exceptionally short nasals (a derived character). The anterior ends of the nasals in *Parabalaenoptera baulinensis* extend anteriorly farther than the anterior margin of the supraorbital processes. Using the supraorbital process as a point of reference for comparison with living balaenopterids, only in the blue whale

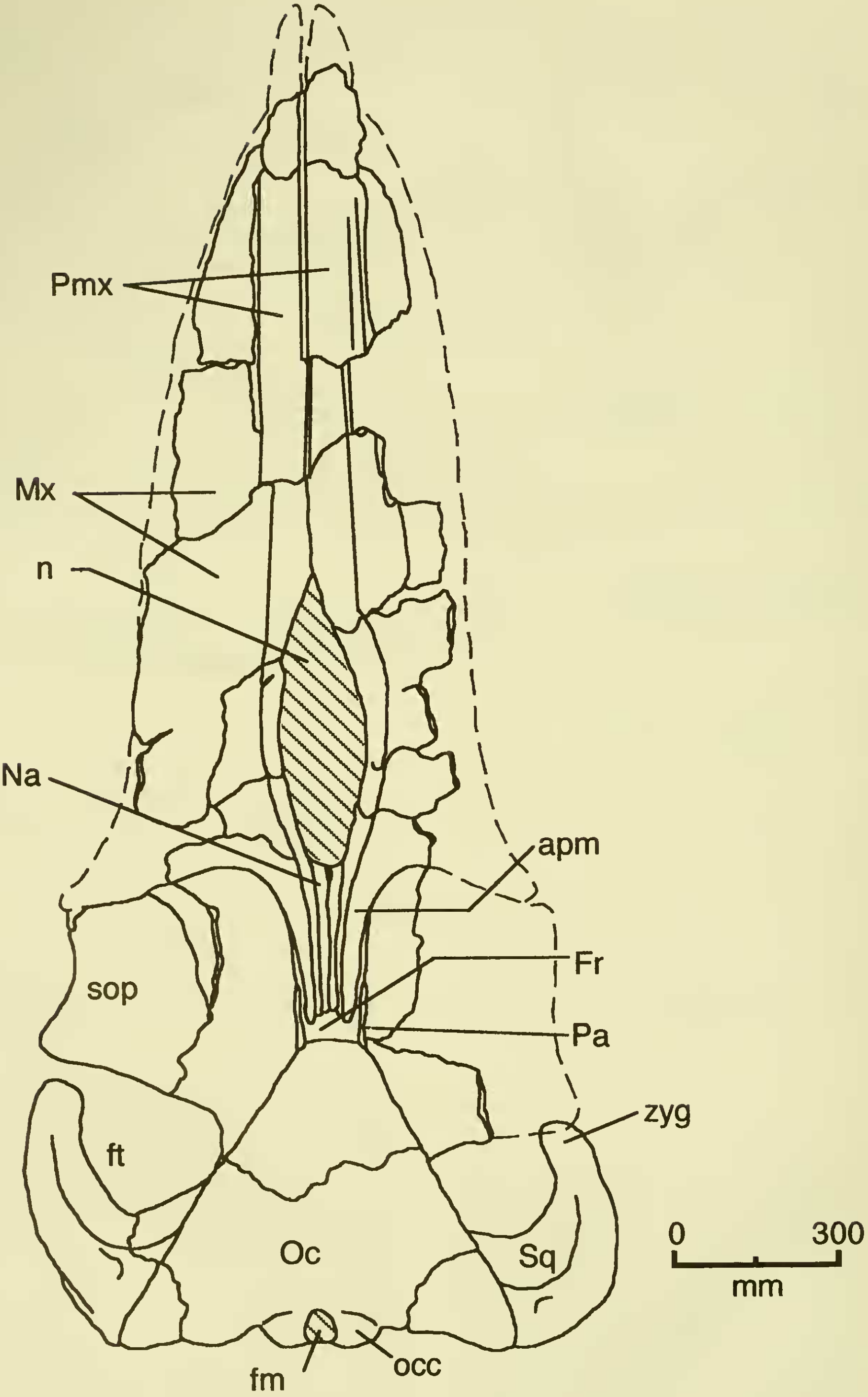

FIGURE 6. *Parabalaenoptera baulinensis*, new genus and species, dorsal view of holotype cranium, CASG 66660; see MATERIALS AND METHODS for abbreviations.

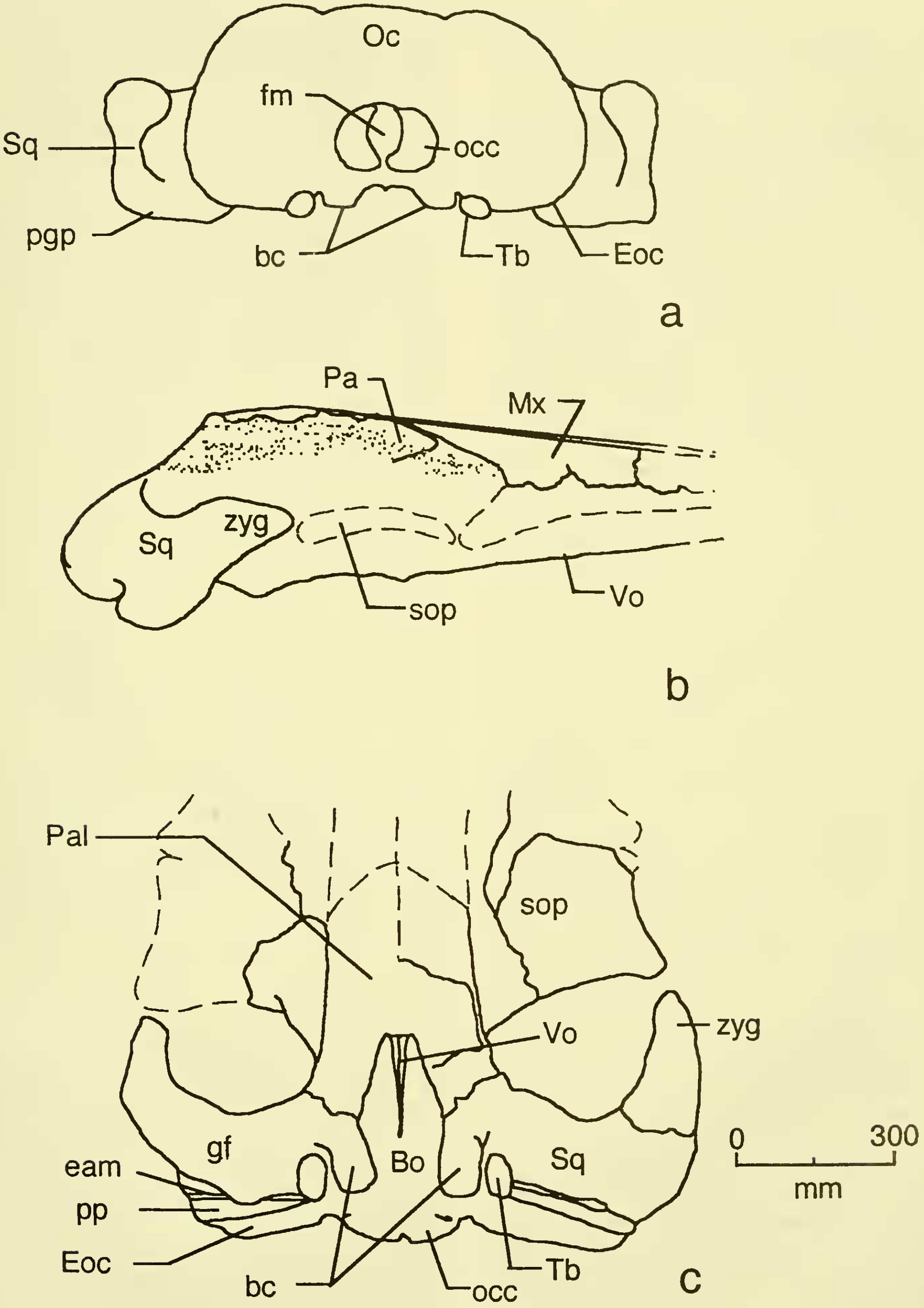

FIGURE 7. *Parabalaenoptera baulinensis,* new genus and species, braincase of holotype, CASG 66660; a. posterior view; b. lateral view; c. ventral view; see MATERIALS AND METHODS for abbreviations.

Balaenoptera musculus (Linnaeus, 1758); see Fig. 8g) do the nasal bones extend more posteriad.

Concomitant with the elongate nasals is the conspicuously anterior position of the narial opening, which has its maximum width of 140 mm at a point 180 mm anterior to the anterior ends of the nasals. The dorsoventral depth of the narial opening at this point, from the dorsal surfaces of premaxillae to the vomer, is 135 mm. The anteroposterior diameter of the narial opening, taken from the point of divergence of the premaxillae to the anterior ends of the nasals, is 520 mm. The choanae, ventral to the nasals, are filled with matrix and not visible for inspection.

Both supraorbital processes of the frontals are fragmented, especially the right process, which crumbled during excavation; however, the left supraorbital process is nearly complete (Fig. 6). Unfortunately, the relationship of the antorbital process to the lacrimal bone cannot be determined as the lacrimal bones are both missing. As is typical of balaenopterids, the supraorbital process is broad, somewhat flat, approximately rectangular in dorsal view, and its dorsal surface slopes ventrally away from the higher cranial vertex. The supraorbital process is broad anteroposteriorly at its medial part. The lateral orbital margin is moderately arched dorsally. The flat plate of the supraorbital process is very long anteroposteriorly at the base and is abruptly depressed well below the dorsal level of the interorbital region. The lateral margin of the supraorbital process is slightly arched over the orbit, and the postorbital process is small as in Recent balaenopterids. The optic nerve canal is enclosed proximally, but as it proceeds laterally, the canal opens and flares out to form the slightly arched roof of the orbit.

In the intertemporal region the parietals are swollen on either side of the frontals and conspicuously raised laterally above the nearly vertical lateral margins of the interorbital region. An anterior projection of the anteroexternal portion of the parietals extends over the frontals on either side of the intertemporal region and the cranial vertex, and they extend on either side of the intertemporal region anteriorly beyond the posterior ends of the nasals, the premaxillae, and ascending processes of the maxillae.

The cranial vertex has the typical configuration of a balaenopterid, with the rostral bones deeply interdigitating with the frontals. There is a small, somewhat rectangular exposure of the frontals on the vertex, but it is still larger than in any Recent balaenopterid (Fig. 8). The narrow (for a balaenopterid) interorbital part of the frontals is exposed between the posterior ends of the nasals, the maxillae, and the premaxillae.

The triangular occipital shield tapers to a truncated apex, which extends anteriorly to a point beyond the level of the anterior extremities of the zygomatic processes of the squamosals, approaching a line drawn transversely through the centers of the orbits. The anterior extent of the supraoccipital shield and the parietals in *P. baulinensis* exceeds that of *B. musculus*, and closely approaches that of the other Recent species of Balaenopteridae. The apex of the occipital shield is not clearly defined, due to apparent abrasion prior to deposition. The essentially straight lateral margins of the occipital shield project laterally over the temporal fossae. There is no concavity to the lateral margin of the occipital shield such as is present in all living species of *Balaenoptera* (Fig. 8). The mid-part of the occipital shield is depressed, attaining a maximum depression of 85 mm below the lateral margins. A lambdoidal crest, formed by the conjunction of the lateral margins of the supraoccipital with the posterior margins of the squamosals and the parietals, arcs dorsomedially toward the truncated apex of the supraoccipital shield. The braincase of *P. baulinensis* is shallow dorsoventrally (Fig. 5), notwithstanding the geologic compression of the skull. The wide exoccipitals flare ventrolaterally (Fig. 7a). The exoccipitals protrude only slightly beyond the posterior margin of the squamosal, and comprise the posterolateral corners of the cranium.

The parietal suture with the squamosal is obscure, however, where the parietal overrides the supraorbital process of the frontal, the boundaries of this bone can be traced. The anterior-most extension of the parietal lies 100 mm distal to the posterior level of the ascending process of the maxilla.

The zygomatic process of the squamosal is large, excavated ventrally, and arches upward at a steep angle from the shallow postglenoid process. It terminates in a stout, anteromedially-directed anterior tip.

The occipital condyles are widely separated dorsally, but are closely approximated ventrally.

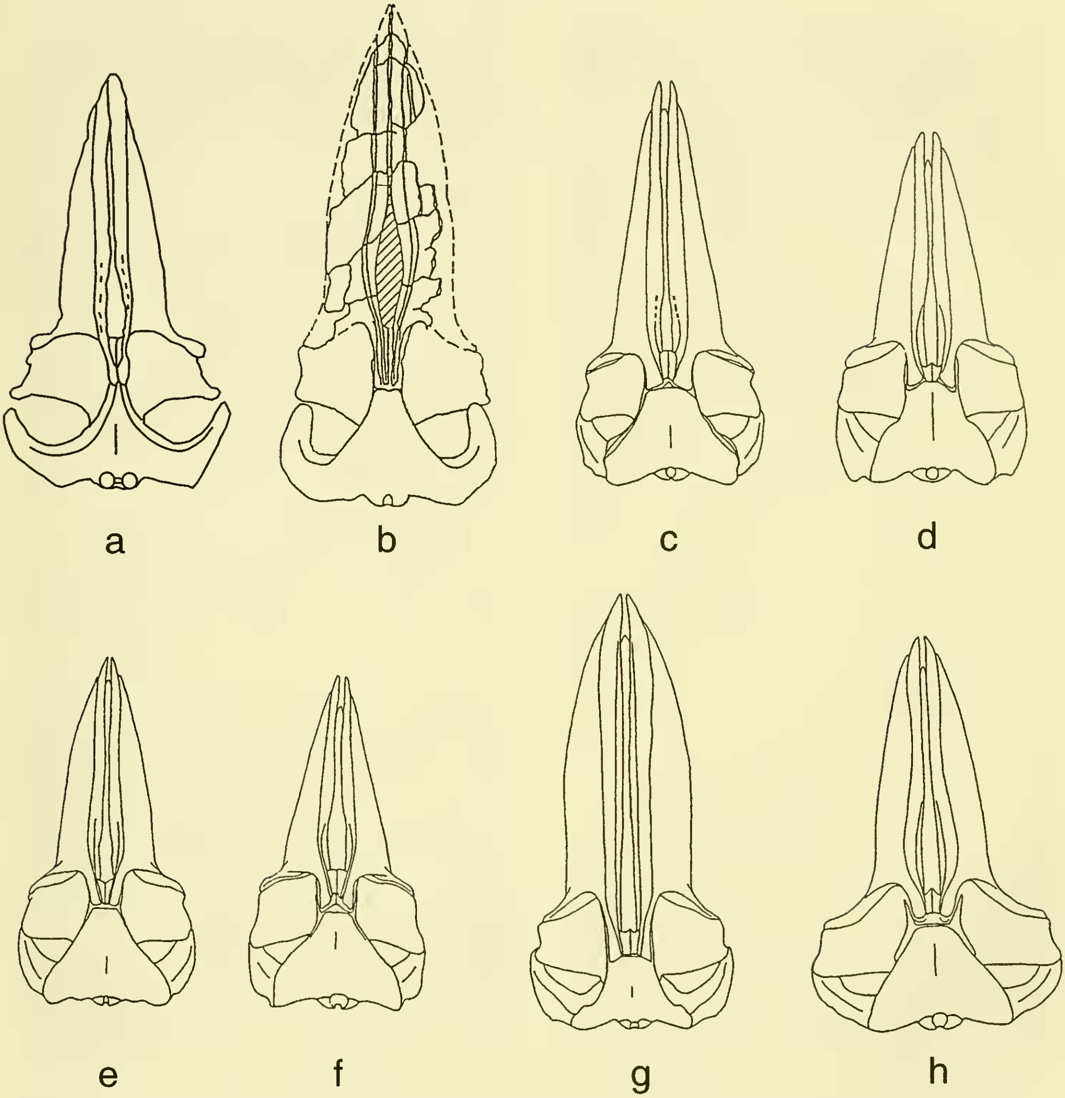

FIGURE 8. Dorsal views of skulls of fossil and Recent Balaenopteridae; a. *Plesiocetus cortesii* (after Van Beneden, 1875:fig. 1); b. *Parabalaenoptera baulinensis*, new genus and species; c. *Balaenoptera borealis* (after Miller, 1924b:pl. 1); d. *Balaenoptera physalus* (after True, 1904:pl. 1, fig. 3); e. *Balaenoptera edeni* (after Omura, 1959:pl. 1, fig. 1); f. *Balaenoptera acutorostrata* (after True, 1904:pl. 22, fig. 1); g. *Balaenoptera musculus* (after Miller, 1924a:pl. 1); h. *Megaptera novaeangliae* (after True, 1904:pl. 29); not to scale.

Their articular surfaces are narrowest dorsally and broadest near the ventral margin of the foramen magnum. There is a slight constriction or neck around the bases of the occipital condyles, which have slightly rugose articular surfaces. The foramen magnum is posterodorsally oriented.

The flat ventral surfaces of the basioccipital crests are on the same plane as the ventral margins of the exoccipitals. The postglenoid processes (these are wide but very shallow dorsoventrally), extend only about 30 mm ventrally. Although there is some evidence of minor abrasion of the ventral surface of the postglenoid processes, it is not enough to affect their dorsoventral dimension.

A vertically oriented slot-like *foramen pseudovale* (37 mm × 13 mm) is open anterolaterally as in Recent rorquals. It is located in the squamosal immediately above the ventral juncture with the pterygoid at about the same level as the anterior margin of the scaphoid fossa.

The ventral surface of the rostrum is not as complete nor as well preserved as the dorsal surface. The infraorbital processes of the maxillae, characteristic of all mysticetes, have been broken off and are missing. The boundaries of the palatines can only be barely discerned, but their anterior and lateral margins can be faintly traced. Their posterior margins are obscure, except for the divergent medial margins that reveal a shallow vomer (20 mm deep at this point), which forms the vertical septum between the narial passages (Fig. 7c). The relatively small cross-sectional area of the nasal choanae is a primitive condition, and may indicate a less efficient diving ability compared to the living rorquals. The exposed vomer septum, extending posteriorly on the basicranium, decreases in height posteriorly until it disappears approximately 220 mm from the posteromedial margins of the palatines.

The distributions of some of the basicranial bones are unclear because of fusion of the sutures between them and the incomplete preservation. The basioccipital is transversely concave between the descending basioccipital crests, which have relatively flat ventral surfaces and have a dorsoventral dimension of 57 mm. The greatest transverse distance between the medial margins of the ventral surfaces of the basioccipital crests is 116 mm.

Both tympanic bullae were recovered and the left bulla remains in place in the basicranium. The right bulla measures 80 mm anteroposteriorly, 52 mm transversely, and 41 mm in depth. The tympanic bullae extend approximately 10 mm below the basioccipital crests (Fig. 7a). The relatively long posterior processes of the periotics are wedged between the squamosals and exoccipitals (Fig. 7c).

The postglenoid process is broad transversely and very shallow dorsoventrally. The slightly posteriorly directed postglenoid process obscures (in ventral view) the central part of the deep external acoustic meatus. This meatus is straight and is almost at 90° to the sagittal plane. The zygomatic process of the squamosal projects laterally and anteriorly about 45° to the sagittal plane of the cranium. It arches dorsally, terminating in an enlarged, medially directed anterior extremity.

The occipital condyles do not extend so far posteriorly as do the posterolateral corners of the exoccipitals. The exoccipitals are very compressed anteroposteriorly, being not much thicker in this dimension than the lateral end of the posterior process of the periotic.

Dentary. — Both dentaries (Figs. 4, 5) are nearly complete, except for a ± 100 mm section of the right horizontal ramus about 120 mm from the anterior tip, and a few small fragments missing from the coronoid processes and the dorsal margins along the dental foramina (see Table 2).

There is evidence that the left dentary was broken in life. An apparent fracture (Fig. 4) is located about 550 mm from the anterior end. It appears that the break was at least partially healed, leaving a ± 25 mm offset of the anterior portion. Subsequent transverse fracturing of the fossilized bone in this area is unclear. The injury

TABLE 2. Measurements (in mm) of right dentary of holotype of *Parabalaenoptera baulinensis*, new genus and species.

1. Greatest length of dentary along outside curvature	2340±
2. Greatest length of dentary in a straight line	2240±
3. Greatest vertical diameter of dentary at level of symphysis	74
4. Greatest transverse diameter of dentary at level of symphysis	47
5. Greatest vertical diameter of dentary at a point 850 mm anterior to hinder face of condyle.	150
6. Greatest vertical diameter of dentary at coronoid process	124
7. Least vertical diameter of dentary behind coronoid process	245
8. Greatest vertical diameter of condyle	180
9. Greatest transverse diameter of condyle	127
10. Greatest dorsoventral diameter of portal to mandibular canal	66
11. Greatest transverse diameter of portal to mandibular canal	43

to the left dentary might account for its being more slender than the right dentary.

Seven nutrient foramina (Figs. 4, 5) are located along the dorsolateral side of each dentary. The spacing between these foramina varies between the two dentaries.

The dentary is conspicuously bowed laterally (Figs. 4, 5), with no evidence of torsion or lateral flattening of the anterior portion. It increases in transverse thickness very gradually to about the level of the posterior margin of the coronoid process, where it then narrows to become constricted between the coronoid process and the mandibular condyle.

In addition to the difference in thickness between the two dentaries, the coronoid regions of the two dentaries show some differences. The right coronoid process is somewhat longer anteroposteriorly, and has a greater lateral curvature than does the left. This difference in curvature is probably due to distortion pressure from the left that straightened the left coronoid, while exaggerating the curvature of the right coronoid (Fig. 5). If this is the case, the distortion was very uniformly distributed, because the outward arc of the right coronoid process is smooth throughout its entire length.

At a point on the dentary about two-thirds of its length from the anterior tip, the coronoid crest begins its long, sloping elevation from the dorsal margin of the ramus. As the dorsal margin of the coronoid crest sweeps gradually upward, it also begins arcing laterally. At its apex, the coronoid process forms a pointed and posteriorly directed tip creating a boss (Fig. 5).

The fossa that is confluent with the mandibular foramen begins near the mandibular condyle, and is directed slightly ventrally, and deepens as it progresses anteriorly. At a point just posterior to the coronoid process, the mandibular foramen enters the dentary with an arch-like margin curving smoothly ventrally and slightly posteriorly; consequently, there is no notch in the anterior margin of the foramen as in *Balaenoptera* and *Megaptera*.

Vertebrae. — The preserved anterior part of the vertebral column includes the seven cervicals, fifteen thoracic vertebrae in series, and an isolated lumbar vertebra. The centra of these vertebrae are mostly well preserved and show little evidence of abrasion.

The centra of vertebrae in the thoracic and lumbar regions are uniformly separated by matrix that filled the inter-vertebral spaces. The neural arches are only fragmentary and the transverse processes have been broken away from the centra of most of the vertebrae. Cervicals 6 and 7, and the first and second thoracic vertebrae remain in a block of concretionary matrix. The vertebral epiphyses are completely fused to all of the centra, indicating that the holotype was an adult individual.

Atlas. — The neural arch of the atlas (see Table 3) is missing, as is the right parapophysis. The posterior articular surfaces are convex. Along the ventral margin of the atlas is a lip-like projection, most prominent at the midline, which extends posteriorly a short distance under the ventral surface of the axis, and conforms closely to the contours of the latter. The imperforate left trans-

TABLE 3. Measurements (in mm) of atlas of holotype of *Parabalaenoptera baulinensis*, new genus and species.

Greatest breadth across transverse processes	354±
Distance ventral margin midline to dorsal margin adontoid fossa	50
Greatest height of right anterior articular surface	150
Greatest breadth of right anterior articular surface	85
Greatest breadth of left anterior articular surface	75
Greatest transverse diameter of neural canal	80
Maximum breadth across posterior articular surfaces	218
Greatest height of right posterior articular surface	111
Greatest height of left posterior articular surface	111
Greatest breadth of right posterior articular surface	80
Greatest breadth of left posterior articular surface	80
Greatest anteroposterior diameter	68
Maximum anteroposterior diameter at ventral midline	57

TABLE 4. Measurements (in mm) of axis of holotype of *Parabalaenoptera baulinensis*, new genus and species.

1. Greatest breadth across transverse processes	500±
2. Height of right transverse process at exterior margin of transverse foramen	143
3. Height of left transverse process at exterior margin of transverse foramen	130
4. Transverse diameter of right transverse foramen	67
5. Transverse diameter of left transverse foramen	62
6. Dorso-ventral diameter of right transverse foramen	38
7. Dorso-ventral diameter of left transverse foramen	32
8. Distance of external margin right articular surface to internal margin right transverse foramen	12
9. Distance of external margin left articular surface to internal margin right transverse foramen	15
10. Greatest breadth of anterior articular surfaces	204
11. Height of right anterior articular surface	121
12. Height of left anterior articular surface	120
13. Maximum extension of odontoid process above the posteriormost level or articular surface	18
14. Distance of anteriormost margin of odontoid process above midline ventral margin	50
15. Greatest posterior transverse diameter of centrum	160
16. Greatest posterior dorsoventral diameter of centrum	111
17. Greatest anteroposterior diameter of centrum at dorsal level	50
18. Greatest anteroposterior diameter of centrum at ventral level	37±

verse process is short and stout, tapering to a rounded end. This process extends 55 mm beyond the lateral margin of the left posterior articular surface at a level slightly below the dorsal margin of this facet.

Axis. — The neural arch of the axis (Table 4) and a small portion of the right transverse process are missing. There is a rudimentary odontoid process projecting anteriorly only 18 mm from the concave anterior articulating surfaces. The long and deep, wing-like, transverse processes are posteriorly deflected approximately 30° from the transverse plane of the centrum.

Third to Seventh Cervical Vertebrae. — The third cervical (see Table 5) is a very fragile vertebra compared to the robust axis. The superior and inferior transverse processes meet to delineate the relatively large transverse foramen. The left foramen has an estimated transverse diameter of 100 mm and a dorsoventral diameter of 75 mm. The neural canal is 95 mm in transverse diameter. The greatest breadth across the transverse processes would appear to approach that of the axis.

The fourth cervical is the most anteroposteriorly compressed cervical vertebra. Its neural canal has an estimated dorsoventral diameter of 50 mm and an estimated transverse diameter of 95 mm.

The fifth cervical vertebra reverses the trend of anteroposterior compression from the atlas toward cervical 4, with the sixth and seventh cervicals becoming progressively thicker anteroposteriorly. The neural arches are crushed upon the centra of all three of these vertebrae.

Thoracic and Lumbar Vertebrae. — Due to the fragmentary condition or absence of transverse processes on the series of 15 vertebrae posterior to the cervicals, it is not possible to determine the transition point from the thoracic to lumbar vertebrae. It is possible that the series are all thoracic vertebrae, inasmuch as the numbers of thoracic vertebrae in balaenopterid whales range from 11 to 15 (Kellogg 1925). With this variability in mind, we refer to the vertebrae as the thoracic-lumbar series (Table 6); the more complete twelfth vertebra in that series is treated more extensively (Table 7). The first thoracic has a centrum that is larger dorsoventrally than any others in the thoracic-lumbar series, 3 through 15, and the width of the anterior face of its centrum is exceeded only slightly by the second thoracic. There is a progressive increase in length of the centra posteriorly in the column. The isolated lumbar vertebra is smaller in all dimensions compared with the last vertebra in the preceding series.

TABLE 5. Measurements (in mm) of cervical vertebrae 3–7 of holotype of *Parabalaenoptera baulinensis,* new genus and species.

Cervical vertebrae	C-3	C-4	C-5	C-6	C-7
1. Length of centrum at dorsal level	41	35	39	40	–
2. Height of anterior face of centrum	105	123	155	150	150±
3. Width of anterior face of centrum	157	150	–	163	160±
4. Length of centrum at ventral level	38	34	–	41	47

Ribs. — The ribs are very fragmentary, but parts of eight right ribs and one left rib have been assembled. The right rib that was found adjacent to the right humerus measures 820 mm in length along its exterior margin. The narrowest part of this rib is at the neck, where it measures 26 mm anteroposteriorly, and the thickest part of this rib in this dimension is 43 mm, midway between the tuberosity and the exterior margin of the angle. In anterior view the rib is widest (80 mm) at the angle, and the transverse diameter at the broken distal portion is 68 mm.

Scapula. — Only fragments of the left scapula were collected. The largest of these is the distal portion of the scapula bearing the glenoid area. The glenoid fossa has a maximum anteroposterior diameter of 150 mm. There is a protuberance with a broken surface about 20 mm above the anterior margin of the glenoid fossa that may be the base of the coronoid process; it is directed anteriorly and slightly medially.

Humerus. — Both humeri are relatively intact and are fairly complete (Table 8). The margins of the tuberosities and distal portions are eroded and a small central section of the left shaft is missing. The large, globular head is smooth and connected by a short but prominent neck to the shaft, which is quite flat mediolaterally. The distal end has two trochlear facets, which are slightly concave, for articulation with the radius and ulna. On the right humerus, the radial facet is at an angle of approximately 48° to the plane of the ulnar facet. Erosion has made it difficult to estimate the dimensions of the trochlea.

DISCUSSION

Balaenopterid Taxonomy and the Problem of Disparate Parts

Not all named fossil balaenopterids are based on directly comparable elements. Regarding mysticete taxonomy, Kellogg (1931) has stated that the classification of fossil taxa must be based upon cranial characters, an opinion that was shared by Barnes (1976). For our comparisons, we examined 14 fossil species of mysticetes in 14 genera. Nine of these species are represented by parts of the cranium, and three of these also include parts of dentaries. The remaining five species are represented by only a single dentary or by parts of dentaries. In contrast, the holotype of *P. baulinensis* is represented by about 90% of the cranium and dentaries, along with both humeri and 23 vertebrae, making it one of the most complete fossil mysticete specimens yet described. Because of its completeness, it was possible to compare it to and distinguish it from all other relevant mysticete taxa.

Other Described Fossil Balaenopterids

Fossil balaenopterids are relatively abundant in late Cenozoic marine deposits around the world (Barnes 1976). In publications, some of these fossils have been assigned to living genera, but have not been more precisely identified. Most of these less precisely identified fossils are clearly referable to the subfamilies Balaenopterinae and Megapterinae and are not directly relevant to the present study. It is, however, necessary to consider previously named balaenopterids in arguing that *Parabalaenoptera baulinensis* is a previously unrecognized taxon in a new subfamily.

The extinct balaenopterids that were described by Van Beneden (e.g., 1872, 1880, 1882, 1885)

TABLE 6. Measurements (in mm) of thoracic-lumbar series of vertebrae of holotype of *Parabalaenoptera baulinensis*, new genus and species.

Thoracic-lumbar vertebrae	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. Length of centrum at dorsal level	–	–	70	98	105	115	–	130	132	136	140	145	152	158	162
2. Height of anterior face of centrum	160±	–	112	112	130	130	130	128	125	129	128	129	133	–	130
3. Width of anterior face of centrum	165±	168±	145	164	160	160	160	157	150	157	162	160	–	136	155
4. Length at ventral level	62	75	87	87	98	120	120	125	–	134	132	131	153	152	158

TABLE 7. Measurements (in mm) of 12th vertebrae of dorsal-lumbar of holotype of *Parabalaenoptera baulinenis*, new genus and species.

Distance from front of anterior zygapophysis to posteriormost margin of neural spine	~190
Distance from level of ventral margin anterior face of centrum to dorsal level of anterior zygapophysis	205
Greatest dorsoventral diameter of neural canal at anterior dorsal margin of centrum	60
Greatest transverse diameter of neural canal	55
Greatest length of neural canal	100
Greatest width of neural spine at dorsal base of anterior zygopophysis	27
Length of base of right transverse process	115
Height of base of right transverse process	34

TABLE 8. Measurements (in mm) of humeri of holotype of *Parabalaenoptera baulinensis*, new genus and species.

	Right	Left
1. Greatest length	305	—
2. Greatest width posterior margin of shaft to anterior margin of greater tuberosity	—	135
3. Anteroposterior diameter of distal end	—	~130
4. Exterointernal diameter of distal end	—	67
5. Anteroposterior diameter of head	132	130
6. Proximal-distal diameter of head	101	115

from the Antwerp Basin in Belgium belong to the closely related balaenopterine genera *Balaenoptera* and *Burtinopsis*, to the megapterine genus *Megaptera*, and to the primitive balaenopterid genus *Plesiocetus* Van Beneden, 1859. Most of the species that Van Beneden described are based on rather complete associated skeletons, but in most cases the specimens include only parts of the crania and mandibles. Included among the Belgian fossils are the extinct balaenopterines *Balaenoptera musculoides* Van Beneden, 1880; *Balaenoptera borealina* Van Beneden, 1880; and *Balaenoptera rostratella* Van Beneden, 1880; and the closely related species *Burtinopsis similis* Van Beneden, 1872, and *Burtinopsis minutus* Van Beneden, 1880. *Balaenoptera musculoides* and *B. borealina* both have parallel dorsal and ventral margins of the horizontal ramus of the dentary, without the long ascending coronoid crest that characterizes *Parabalaenoptera baulinensis*, and in this regard they are like the living species of *Balaenoptera*. Likewise, *B. rostratella* has characters of the genus *Balaenoptera*, and is approximately one-half the size of *Parabalaenoptera baulinensis*. Species of *Burtinopsis* are similar to *Balaenoptera*, and in fact, Deméré (1986) has considered *Burtinopsis* to be a junior synonym of *Balaenoptera*.

Because the known morphologies of these fossil balaenopterids are consistent with those of the living species of *Balaenoptera* and *Megaptera*, we accept Van Beneden's original generic allocations for them and assign them to the subfamilies Balaenopterinae and Megapterinae, respectively. Each of them can be distinguished from *Parabalaenoptera* by the characters that we use to diagnose the subfamily Parabalaenopterinae (Table 9).

A species in the supposed balaenopterid genus *Mizuhoptera* Hatai, Hayasaka, and Masuda, 1963, was described on the basis of isolated tympanic bullae of Pliocene age from Japan. Oishi and Hasegawa (1995) concluded that the type material actually represents the cetotheriid genus *Herpetocetus* Van Beneden, 1872. Therefore, the genus *Mizuhoptera* is invalid and is not a balaenopterid.

A Late Miocene mysticete, *Balaenoptera ryani* Hanna and McLellan, 1924, from the Monterey Formation in central California, was named

TABLE 9. Differences between Parabalaenopterinae, new subfamily, and the subfamilies of Megapterinae and Balaenopterinae.

	Parabalaenopterinae	Megapterinae and Balaenopterinae
CRANIUM		
1. Cranial vertex	narrow	broad
2. Nasals	long, narrow	short, broad
3. Shape of ascending process of maxilla	cuneate	flared
4. Anterior portion of parietal	raised, swollen	flat, feathered
5. Postglenoid process	shallow	deep and moderately deep
DENTARY		
6. Length of coronoid ridge anterioposteriorly relative to mandible length	long	short
7. Direction of terminus of coronoid process	posterior	dorsal
8. Terminus of coronoid process	bullet-shaped boss	smoothly tapered
9. Mandibular foramen	lacks notch	notched

on the basis of a braincase. It is not a member of the genus *Balaenoptera,* and is not even a balaenopterid. Instead, it is a typical cetotheriid (see Barnes, 1976:330) because its parietals are exposed in a wide band across the top of the intertemporal region, and it does not have the type of interfingering of the rostral and cranial bones that is diagnostic of the family Balaenopteridae.

Only two fossil species of balaenopterids have been previously named from the Pacific coast of North America. *Megaptera miocaena* Kellogg, 1922, from the Late Miocene Monterey Formation in Santa Barbara County, California, is a large species of balaenopterid (Barnes, 1976:329). It has short and wide nasal bones and a wide intertemporal region like both *Megaptera* and *Balaenoptera,* but the concave lateral margins of its occipital shield are like members of the subfamily Balaenopterinae. Its zygomatic arches are relatively narrow, a primitive character, and it appears to be a primitive species of the subfamily Balaenopterinae.

Balaenoptera davidsonii Cope, 1872, is a small mysticete from the Late Pliocene age San Diego Formation at San Diego, California. It was first named as a species of *Eschrichtius* (gray whales), but Barnes (1976:333, table 6) removed it from the Eschrichtiidae, pointing out that the holotype dentary did not have characters of the family, and Deméré (1986) placed it in the genus *Balaenoptera.* Thus, both previously named fossil balaenopterids from the eastern North Pacific realm are apparently members of the subfamily Balaenopterinae.

The Relationships of *Parabalaenoptera baulinensis*

Parabalaenoptera baulinensis is demonstrably a member of the family Balaenopteridae, which includes the living humpback (*Megaptera novaeangliae* (Borowski, 1781)), various species of rorquals of the genus *Balaenoptera,* and various extinct taxa as mentioned above. *Parabalaenoptera baulinensis* possesses six derived cranial characters and one derived mandibular character that are diagnostic of the family Balaenopteridae (see also Miller 1923; Kellogg 1931). These derived characters, which define the family Balaenopteridae, are listed in the legend (Node 1) of the cladogram (Fig. 9), and are discussed as follows:

1) The parietals are excluded from medial exposure on the dorsal surface of the intertemporal region, but they extend anteriorly along either side of the frontals at least to a point beyond the posterior ends of the rostral bones (the nasals, maxillae, and premaxillae).

2) The apex of the occipital shield extends anteriorly at least as far as the level of the poste-

rior border of the supraorbital process and the anterior extremity of the zygomatic process of the squamosal.

3) The frontal has only a small exposure on the middle of the dorsal surface of the interorbital region.

4) The lateral part of the squamosal is relatively large and expanded, and the postglenoid process is large.

5) The dorsal surface of the supraorbital process of the frontal is very depressed medially, descending abruptly from the more elevated dorsal surface of the interorbital region.

6) The maxillary part of the rostrum is transversely expanded and relatively flat, except in its median part, which has a keel that is created by the vomer, and is not conspicuously arched anteroposteriorly.

7) The dentary is conspicuously bowed laterally, beyond the curvature of the rostral margin.

Parabalaenoptera baulinensis has five primitive characters that exclude it from the derived subfamilies Balaenopterinae and Megapterinae, and these contribute to the definition of the new subfamily Parabalaenopterinae. These five characters are discussed as follows:

1) The narrow intertemporal region of *Parabalaenoptera baulinensis* is a retained primitive character that is shared with members of the family Cetotheriidae and with the primitive balaenopterid *Plesiocetus cortesii* (Capellini, 1865) (see discussion of *Plesiocetus* below). Members of the Balaenopterinae and Megapterinae (see Kellogg 1928; Barnes and McLeod 1984) have relatively wider intertemporal regions than *P. baulinensis*, in some cases wider by a factor of more than two.

2) The dorsal exposure of the frontals on the middle of the dorsal surface of the intertemporal region between the posterior ends of the rostral bones and the apex of the occipital shield in *Parabalaenoptera baulinensis* is relatively large for a balaenopterid, forming an approximately rectangular patch. This larger exposure is a primitive character that is shared with members of the family Cetotheriidae, and contrasts with the much reduced and nearly absent dorsal exposure of the frontals in skulls of animals in the subfamilies Balaenopterinae and Megapterinae.

3) The nasals of *Parabalaenoptera baulinensis* are longer (4:1 length to width ratio) than those of any extant balaenopterid, extending anteriorly to a point anterior to the level of the antorbital notches. In members of the subfamilies Balaenopterinae and Megapterinae, however, the nasals are short and terminate posterior to the level of the antorbital notches. The nasals of *P. baulinensis* are nearly as long as those of such Late Oligocene and Early Miocene cetotheriids (sensu Kellogg 1931) as *Mauicetus parki* (Benham, 1937) (nasal length to width ratio of 5.5:1) and *Aglaocetus moreni* (Lydekker, 1894) (nasal length to width ratio of 5:1). Therefore, the long and narrow nasals of *Parabalaenoptera baulinensis* are a retained primitive character.

4) The posteriorly tapering, narrow, ascending processes of the maxillae of *P. baulinensis* differ from the lobate posterior ends of the maxillae in the Balaenopterinae and Megapterinae. In *P. baulinensis* these processes become progressively more narrow posteriorly and terminate in rounded points. This condition we refer to as "cuneate," in order to distinguish it from the transversely flared or lobate shape of the ascending processes, which was considered by Barnes and McLeod (1984) to be a balaenopterid character. Henceforth, the posteriorly expanded ascending processes of the maxillae shall be considered a derived character that is shared by the subfamilies Balaenopterinae and Megapterinae. The cuneate processes are a primitive character of *Parabalaenoptera baulinensis*, which is shared with cetotheriids, and distinguishes the subfamily Parabalaenopterinae from the two other balaenopterid subfamilies.

5) The short postglenoid process of *Parabalaenoptera baulinensis* is a primitive character that is shared with species of Cetotheriidae and primitive balaenopterids of the genus *Plesiocetus*. It differs from the bulbous postglenoid process of the derived balaenopterids, and is a defining character of the subfamily Parabalaenopterinae.

The derived character states of the above five structures (the opposite polarity of the character states in *Parabalaenoptera baulinensis)* are shared by the subfamilies Balaenopterinae and Megapterinae, and indicate that the latter two are sister taxa. They appear at Node 5 on the cladogram (Fig. 9).

Parabalaenoptera baulinensis has three autapomorphies, which appear at Node 4 in the

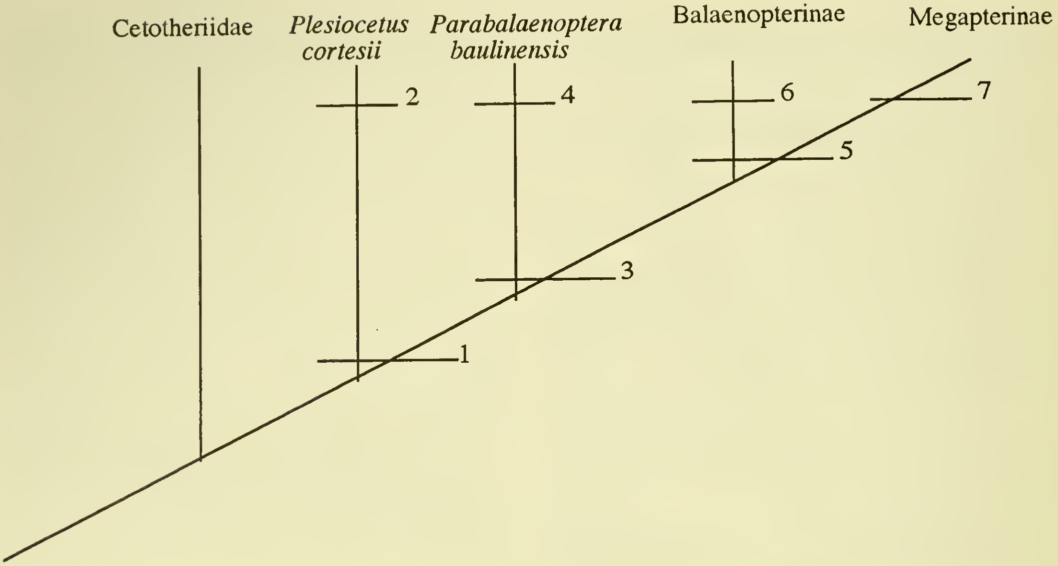

FIGURE 9. Cladogram showing postulated relationships of *Parabalaenoptera baulinensis*, new genus and species, among fossil and Recent Balaenopteridae. The subfamily Cetotheriinae is the outgroup. Characters marking the numbered dichotomies and end points are as follows:

1. Anterior border of supraorbital process of frontal depressed relative to dorsal surface of maxilla and forming a coved recess; parietals excluded from dorsal surface of intertemporal region and extending anteriorly on lateral sides of the frontals in the intertemporal region to a point beyond the posterior ends of rostral bones; apex of occipital shield extended anteriorly at least as far as the level of the posterior border of the supraorbital process and the anterior extremity of the zygomatic process of the squamosal; lateral part of the squamosal relatively large and expanded; supraorbital process of the frontal abruptly depressed at its medial part to a level well below that of the dorsal surface of the interorbital region; dentary conspicuously bowed laterally [family Balaenopteridae].
2. Nasals short, terminating anteriorly at a point posterior to the level of the antorbital notch [*Plesiocetus cortesii*].
3. Contact between the posterior border of the maxilla and the anterior margin of the supraorbital process of the frontal curved anteriorly; postorbital process of frontal reduced; zygomatic process of squamosal inflated and curved medially (concomitant with shorter postorbital process); mandibular condyle spherical and bulbous.
4. Parietal on either side of the intertemporal region swollen and elevated dorsal to the level of the adjacent frontal; coronoid crest of dentary elevated and inclined toward the coronoid process; apex of coronoid process posteriorly directed and spindle-shaped [*Parabalaenoptera baulinensis*].
5. Nasal bones short and terminating posterior to the antorbital notch; posterior end of the ascending process of the maxilla lobate or transversely expanded; intertemporal region expanded transversely; dorsal exposure of the frontals between posterior ends of the rostral bones and apex of the occipital shield reduced; parietals on either side of intertemporal region thin and interfingering with frontals anteriorly; postglenoid process of the squamosal large, bulbous, and extending ventrally from the cranium.
6. Concave lateral margin of the occipital shield where it overhangs the temporal fossa [subfamily Balaenopterinae].
7. Braincase transversely expanded; coronoid process of dentary reduced in size; olecranon process of ulna lost [subfamily Megapterinae].

cladogram (Fig. 9). These contribute to the definition of the taxon, and are discussed as follows:

1) In *Parabalaenoptera baulinensis,* as in all Balaenopteridae, the parietals are excluded from exposure in the dorsal surface of the intertemporal region, and they extend anteriorly along both sides of the frontals to a point as far as the posterior ends of the nasals. However, a unique derived character of *P. baulinensis* is the inflation and elevation of this lateral part of the parietals above the level of the frontals. Both the right and left parietals exhibit this feature to about the same degree, indicating that it is normal and not pathological. This contrasts with the flat, interfingering condition of the parietals in the subfamilies Balaenopterinae and Megapterinae.

2) The long, gradually ascending coronoid crest on the dentary that approaches the coronoid process (see Fig. 5) is a unique derived character of *P. baulinensis*. The structure is absent in all other Balaenopteridae, in which the coronoid process rises abruptly from the straight dorsal

other Balaenopteridae, in which the coronoid process rises abruptly from the straight dorsal margin of the horizontal ramus.

3) The apex of the coronoid process is posteriorly directed and spindle shaped. This is unlike the condition in Cetotheriidae and in the Balaenopterinae and Megapterinae.

To summarize the points above, *Parabalaenoptera baulinensis* is a member of the family Balaenopteridae, because it has the suite of diagnostic osteological characters that are presently used to recognize the family. It also has some plesiomorphic characters that are not present in members of the two highly evolved balaenopterid subfamilies, Balaenopterinae and Megapterinae: narrow intertemporal region, larger exposure of frontal in intertemporal region, long and narrow nasal bones, tapered ascending processes of the maxillae, and short postglenoid process of the squamosal. These primitive characters are shared with members of the family Cetotheriidae, and they add to evidence for derivation of the Balaenopteridae from the Cetotheriidae. *Parabalaenoptera baulinensis* also has three unique derived characters that separate it from other Balaenopteridae: the elevated and swollen parietals on either side of the intertemporal region, the long, ascending coronoid crest anterior to the coronoid process on the dentary, and the spindle-shaped posteriorly-directed apex of the coronoid process. The combination of the five primitive characters and three unique derived characters of *Parabalaenoptera baulinensis* serve to define the taxon and the new subfamily Parabalaenopterinae that contains it.

The Genus *Plesiocetus* Van Beneden, 1859

The family assignment of the extinct mysticete genus *Plesiocetus* Van Beneden, 1859, has varied, and it has been assigned to both the Cetotheriidae and the Balaenopteridae. At least 13 species of Late Miocene and Pliocene age from throughout the world have been assigned to the genus. While it is beyond the scope of the present study to resolve the issues affecting the complicated typology and systematics of *Plesiocetus* and the species that have been assigned to it, it is useful to mention some of the problems that surround it (see also Cabrera 1926; Kellogg 1968:103–104).

Both Winge (1910) and True (1912), who presented a generic diagnosis, considered *Plesiocetus* to be a valid balaenopterid genus, but Kellogg (1968:104) wrote that "Sufficient diagnostic criteria for the recognition of *Plesiocetus* as a valid genus are not presently known." Brandt (1872:407) assigned the genus *Plesiocetus* to what he regarded as the balaenopterid subfamily Cetotheriinae, the group now recognized as the family Cetotheriidae. Van Beneden (1872:242) fixed the type species as *Plesiocetus garopii* Van Beneden, 1859, and considered the genus to be related to balaenopterines. Kellogg (1925:51), however, noting that in 1885 Van Beneden omitted *P. garopii* from a listing of species in the genus *Plesiocetus*, fixed the type species as *Plesiocetus hupschii* Van Beneden, 1859, and discussed it in the context of the family Cetotheriidae. Later (1934:79) Kellogg, restricted the genus name *Plesiocetus* to *Plesiocetus garopii* (Van Beneden's type species), and considered it to be a balaenopterine.

Comparisons with *Plesiocetus cortesii*

Regardless of the status and systematics of the genus *Plesiocetus*, one species that has been referred to the genus is of direct relevance to the present study because it helps to establish the polarity of the characters of *Parabalaenoptera baulinensis* and its taxonomic position. This is the species *Plesiocetus cortesii*, from Pliocene deposits in Italy, the skull and dentary of which were illustrated by Van Beneden (1875).

The skull of *Plesiocetus cortesii* (see Fig. 8a) resembles that of *Parabalaenoptera baulinensis* (see Fig. 8b) in its general proportions, but it differs in some details.

Compared to *Parabalaenoptera baulinensis*, *P. cortesii* (Fig. 8a) has the following more primitive character states:

1) The contact between the posterior border of the maxilla and the anterior margin of the supraorbital process of the frontal is transversely straight rather than curved anteriorly.

2) The postorbital processes of the frontals are larger and project posterolaterally.

3) The occipital shield is smaller and has more nearly the shape of an equilateral triangle.

4) The zygomatic processes are narrower and straighter.

5) The mandibular condyle is smaller and not so spherical.

The derived character states of the above five structures (the opposite polarity of the character states in *Plesiocetus cortesii)* are shared by *Parabalaenoptera baulinensis* and the subfamilies Balaenopterinae and Megapterinae, and indicate that the latter three are sister taxa (Node 3 on the cladogram, Fig. 9).

Compared to *Parabalaenoptera baulinensis, P. cortesii* has nasal bones that are much shorter, terminating at a point posterior to the level of the antorbital notches, and this is a derived character that defines *P. cortesii* and is listed at Node 2 on the cladogram (Fig. 9). The nasal bones are similarly short in Recent Balaenopterinae and Megapterinae, but the nasals of *P. cortesii* differ by being narrower and not expanded anteriorly. Because of the numerous other primitive characters of *P. cortesii,* we conclude that short nasal bones evolved convergently in *P. cortesii* and in both of the derived subfamilies Balaenopterinae and Megapterinae.

Plesiomorphies that *Plesiocetus cortesii* shares with *Parabalaenoptera baulinensis* include the narrow posterior terminations of the maxillae, the narrow anterior ends of the nasals, and the narrow intertemporal region. *Plesiocetus cortesii* is a primitive balaenopterid, and in most of its characters is more primitive than *Parabalaenoptera baulinensis.*

CONCLUSIONS

1. *Parabalaenoptera baulinensis,* a new genus and species of extinct whale in the family Balaenopteridae, is based on a partial fossil skeleton collected from the sea cliff at Bolinas Point, Point Reyes Peninsula, in Marin County, California.

2. The holotype specimen is from the Late Miocene age Santa Cruz Mudstone, and analysis of diatoms from the rock unit indicates an age of between approximately 6.8 and 6.0 Ma.

3. The holotype skeleton includes the skull, both dentaries, cervical, thoracic, and one lumbar vertebrae, pectoral limb bones, and ribs, making this one of the most complete fossil balaenopterid specimens recorded in the published literature. The animal is estimated to have had a total body length of approximately 10 m in life.

4. *Parabalaenoptera baulinensis* is a relatively primitive balaenopterid, and it lacks synapomorphies of the derived balaenopterids of the subfamilies Balaenopterinae and Megapterinae. It has a suite of autapomorphies (conspicuously elevated or swollen anterior portions of the parietals on either side of the intertemporal region, long and ascending coronoid crest on the dentary approaching the coronoid process, and posteriorly-directed apex of the coronoid process), and we classify it in the new subfamily Parabalaenopterinae.

5. *Parabalaenoptera baulinensis* shares symplesiomorphies with the primitive family Cetotheriidae (narrow intertemporal region, larger exposure of frontals on the dorsal surface of intertemporal region, long nasals, long and posteriorly tapering ascending processes of the maxillae, and short postglenoid processes of the squamosals), and these shared primitive characters lend support to the theory that the Balaenopteridae evolved from the Cetotheriidae.

6. Species of the genus *Plesiocetus* Van Beneden, 1859, pose many problems of classification and relationships. One species in the genus, *Plesiocetus cortesii* (Capellini, 1865), is possibly a sister taxon of a less inclusive clade containing *Parabalaenoptera baulinensis,* the subfamily Balaenopterinae, and the subfamily Megapterinae.

7. Because other, more highly derived taxa of Balaenopteridae are contemporaneous with *P. baulinensis,* it may be considered to be a relict descendant of a lineage that was ancestral to both the subfamilies Megapterinae and Balaenopterinae, and thus to the extant *Megaptera* and *Balaenoptera.* The origin of *Parabalaenoptera baulinensis* must lie among pre-Late Miocene mysticetes that are closer in morphology to primitive members of the family Cetotheriidae.

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LITERATURE CITED

BARNES, L. G. 1976. Outline of eastern North Pacific fossil cetacean assemblages. Syst. Zool. 25:321–343.

BARNES, L. G., D. P. DOMNING AND C. E. RAY. 1985. Status of studies on fossil marine mammals. Mar. Mamm. Sci. 1(1):15–53.

BARNES, L. G. AND S. A. MCLEOD. 1984. The fossil record and phyletic relationships of gray whales. Chapter 1. Pp. 3–32 *in* The gray whale: *Eschrichtius robustus.* M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. Academic Press, Orlando, Florida.

BENHAM, W. B. 1937. Fossil Cetacea of New Zealand. II — On *Lophocephalus,* a new genus of zeuglodont Cetacea. Trans. Roy. Soc. New Zealand 67:1–7, pls. 1–7.

BRANDT, J. F. 1872. Bericht über den bereits vollendeten druckfertigen Theil seiner Untersuchungen über die fossilen und subfossilen Cetaceen Europa's. Bull. Acad. Sci. St. Petersburg, Sér. 3, 17:401–408.

CABRERA, A. 1926. Cetáceos fosiles del Museo de la Plata. Rev. Mus. La Plata 29:363–411.

CAPELLINI, G. 1865. Balenottere fossili del Bolognese. Mem. Accad. Sci. Bologna, Ser. 2, 4:315–336, 3 pls.

CLARK, J. C., E. E. BRABB, H. G. GREENE AND D. C. ROSS. 1984. Geology of the Point Reyes Peninsula and implications for San Gregorio fault history. Tectonics and sedimentation along the California margin. Soc. Econ. Paleontol. Mineral., Pacific Sect. 38:67–86.

COPE, E. D. 1872. On an extinct whale from California. Proc. Acad. Natur. Sci. Philadelphia 1872 (part 1):29–30.

DEMÉRÉ, T. A. 1986. The fossil whale, *Balaenoptera davidsonii* (Cope, 1872), with a review of other Neogene species of *Balaenoptera* (Cetacea: Mysticeti). Marine Mammal Science 2(4):277–298.

DOMNING, D. P. 1978. Sirenian evolution in the North Pacific Ocean. Univ. Calif. Publ. Geol. Sci. 18:i–xi, 1–176, pls. 1–18.

DU BUS, B. A. L. 1867. Sur quelques mammifères du Crag d'Anvers. Bull. Acad. Roy. Sci. Belgique, Ser. 2(24):562–577.

FORDYCE, R. E. AND L. G. BARNES. 1994. The evolutionary history of whales and dolphins. Pp. 419–455 *in* 1994 Annual Review of Earth and Planetary Sciences, Volume 22, G. W. Wetherill, ed. Annual Reviews, Inc., Palo Alto, California.

GALLOWAY, A. J. 1977. Geology of the Point Reyes Peninsula, Marin County, California. Calif. Div. Mines Geol. Bull. 202:i–v, 1–72, pl. 1 (map).

HANNA, G D. AND M. E. MCLELLAN. 1924. A new species of whale from the type locality of the Monterey Group. Proc. Calif. Acad. Sci., 4th Series, 13(14):237–241, pls. 5–9.

HATAI, K., S. HAYASAKA AND K. MASUDA. 1963. Some fossil tympanics from the Mizuho period of northern Japan. Saito Ho-on Kai Mus. Natur. Hist. Res. Bull. 32:5-17.

HOWELL, A. B. 1930. Aquatic mammals. Their adaptations to life in the water. Charles C. Thomas, Springfield, Illinois, and Baltimore, Maryland.

KELLOGG, A. R. 1922. Description of the skull of *Megaptera miocaena*, a fossil humpback whale from the Miocene diatomaceous earth of Lompoc, California. Proc. U. S. Natl. Mus. 61(14):1–18, pls. 1–4.

———. 1925. Additions to the Tertiary history of pelagic mammals on the Pacific coast of North America. II. Fossil cetotheres from California. Carnegie Inst. Washington Publ. 348(2):35–56.

———. 1928. The history of whales — their adaptation to life in the water. Quart. Rev. Biol. 3(1,2):29–76, 174–208.

———. 1931. Pelagic mammals from the Temblor Formation of the Kern River region, California. Proc. Calif. Acad. Sci., 4th Series, 19(12):217–397.

———. 1934. The Patagonian fossil whalebone whale, *Cetotherium moreni* (Lydekker). Carnegie Inst. Washington Publ. 447:63–81, pls. 1–4.

———. 1968. Fossil marine mammals from the Miocene Calvert formation of Maryland and Virginia. Part 5. Miocene Calvert mysticetes described by Cope. U. S. Nat. Mus. Bull. 247:103–132.

LYDEKKER, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. 2. Cetacean skulls from Patagonia. An. Mus. La Plata, Sec. Paleontol. (2):1–13, 6 plates.

MILLER, G. S. 1923. The telescoping of the cetacean skull. Smithsonian Misc. Coll. 75(5):1–71, pls. 1–8.

———. 1924a. Some hitherto unpublished photographs and measurements of the blue whale. Proc. U. S. Natl. Mus. 66(7):1–4.

———. 1924b. A pollack whale from Florida presented to the National Museum by the Miami Aquarium Association. Proc. U. S. Natl. Mus. 66(9):1–15.

OISHI, M. AND Y. HASEGAWA. 1995. Diversity of Pliocene mysticetes from eastern Japan. The Island Arc [Thematic Issue: Evolution and Biogeography of Fossil Marine Vertebrates in the Pacific Realm, Proceedings of the 29th International Geological Congress, Kyoto, Japan, edited by L. G. Barnes, Y. Hasegawa, and N. Inuzuka] 3(4):436–452 [for 1994].

OMURA, H. 1959. Bryde's whale from the coast of Japan. Sci. Rep. Whales Res. Inst. 14:1–33.

REPENNING, C. A. AND R. H. TEDFORD. 1977. Otarioid seals of the Neogene. U. S. Geol. Surv. Prof. Paper 992:i–vi, 1–93, pls. 1–24.

TRUE, F. W. 1904. The whalebone whales of the western North Atlantic. Smithsonian Contrib. Knowl. 33:1–332.

———. 1912. The genera of fossil whalebone whales allied to Balaenoptera. Smithsonian Misc. Coll. 59(6):1–8.

VAN BENEDEN, P. J. 1859. Ossements fossiles découverts à Saint Nicolas en 1859. Bull. Acad. Roy. Sci. Belgique, Ser. 2, 8(11):123–146.

———. 1872. Les baleines fossiles d'Anvers. Bull. Acad. Roy. Sci. Belgique, Ser. 2, 34(7):6–20.

———. 1875. Le squelette de la baleine fossile du Musée de Milan. Bull. Acad. Roy. Sci. Belgique, Ser. 2, 40(12):736–758, figs. 1–2.

———. 1880. Les mysticètes à courts fanons des sables des environs d'Anvers. Bull. Acad. Roy. Sci. Belgique, Ser. 2, 50(7):11–27.

———. 1882. Description des ossements fossiles des environs d'Anvers, Troisième Partie, Cétacés. Genres: *Megaptera, Balaenoptera, Burtinopsis & Erpetocetus.* Ann. Mus. Roy. d'Hist. Nat. Belgique, Ser. Paléontologique 7:1–90, pls. 40–109.

———. 1885. Description des ossements fossiles des environs d'Anvers, Quatrième Partie, Cétacés. Genre: *Plesiocetus.* Ann. Mus. Roy. d'Hist. Nat. Belgique, Ser. Paléontologique 9:1–40, pls. 1–30.

WILSON, L. E. 1937. New species of dolphin from Point Reyes, California. Abstract, Proc. Geol. Soc. Amer. 1936:387.

WINGE, H. 1910. Om *Plesiocetus* og *Sqvalodon* [sic] fra Danmark. Vidensk. Meddel. Naturhist. Foren., Copenhagen, 7(1):1–38, pls. 1–2.

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